

Lemmings (Mammalia, Rodentia) as indicators of temperature and humidity in the European Quaternary

Kazimierz KOWALSKI

Accepted for publication: 20 Oct. 1994

KOWALSKI K. 1995. Lemmings (Mammalia, Rodentia) as indicators of temperature and humidity in the European Quaternary. *Acta zool. cracov.*, **38**(1): 85-94.

Abstract. Lemmings (Arvicolidae: Lemminae and Dicrostonychinae) have been generally recognized as excellent indicators of cold climate in the Quaternary of Europe. Lemminae are present in Middle Pliocene localities (*Synaptomys*) accompanied by a Mediterranean-type fauna. The genus *Lemmus* first appeared at the end of the Pliocene (Villanyian) and survived in the now temperate zone of Europe through the climatic oscillations of the Early and Middle Pleistocene, mainly accompanied by a forest fauna. Dicrostonychinae, represented by the lineage *Predicrostonyx* – *Dicrostonyx*, first appeared in the Pleistocene and were always restricted to cold episodes. In the Late Pleistocene both subfamilies were common in the periglacial zone of Europe. The distributions of lemmings in Europe during different periods of the Quaternary are presented and their paleoecological implications are discussed.

Key words: Lemmings, paleoclimate, Quaternary, Europe.

Kazimierz KOWALSKI, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland.

I. INTRODUCTION

At the beginning of the second half of the 19th century three scientists independently identified lemmings among Quaternary remains in temperate latitudes of Western Europe: POMEL in 1853 in France, HENSEL in 1855 in Germany and SANFORD in 1872 in England. The presence of lemmings, typical inhabitants of the Recent arctic tundra, was soon recognized as the best evidence of the existence of Ice Ages and of arctic conditions in now temperate regions of Europe.

In later years many paleontologists have been of the opinion that rodents and particularly voles are excellent indicators of paleoclimatic conditions. It is interesting to review the relationship between the rodent fauna and the character of the Quaternary paleoenvironment in Europe. Lemmings may be a good example of this relationship.

The common name lemmings is used for two subfamilies of Arvicolidae, Lemminae and Dicrostonychinae, which are characterized by a short lower incisor and are inhabitants

of arctic and boreal zones of the Holarctic. The two subfamilies originated independently from unknown ancestors and were the first arvicolids to develop permanently growing molars (KOENIGSWALD & MARTIN 1984).

II. LEMMINAE

Lemminae probably originated in Asia. Their earliest representatives are placed in the genus *Synaptomys*, and appeared at about the same time in the Middle Pliocene of Europe and North America (SUKHOV 1976, KOWALSKI 1977). In Europe, *Synaptomys* disappeared at the end of the Ruscinian, while in America it has survived until the present day, mainly populating humid, boreal forests.

Lemmus probably originated in boreal regions of the Western Palaearctic. Its earliest remains are known from Europe, but it later spread to Asia and Alaska, where it was present in the Cape Deceit fauna among others (GUTHRIE & MATTHEWS 1971). Its further expansion in the arctic zone of North America is of very recent date (BURNS 1980).

Morphological evolution of the molars in Lemminae was very slow. Lemmings from the Villanyian were described as *Lemmus kowalskii* CARLS & RABEDER, 1988; this species was also recognized by HARRISON et al. (1989) at Sidestrand in England. In other Villanyian and Early Pleistocene localities lemmings were usually listed as *Lemmus* sp. and in Middle and Late Pleistocene localities as *Lemmus lemmus* or *Lemmus sibiricus*. These two last species are morphologically very similar and impossible to distinguish in fossil material; their speciation may be of relatively recent date. Fossil remains of *Lemmus* (*Myopus*) *schisticolor* have never been definitely identified in the European Pleistocene. Perhaps this species, now associated with coniferous forests and known as a fossil from Japan, did not reach Europe before the beginning of the Holocene.

The earliest immigration of *Lemmus* in Europe took place in the Villanyian. The age of the localities with *Lemmus* remains may be slightly different, but they all contain several species of *Mimomys* and have neither *M. savini* nor *Allophaiomys*. The oldest of these localities seems to be Osztramos 7 (JÁNOSSY 1973), with a fauna indicative of a mild climate (presence of *Hystrix* and numerous glirids). Another Hungarian locality with *Lemmus*, Osztramos 3, may be slightly younger. Montoussé 5 in the Pyrénées contains a fauna of similar age (CLOT et al. 1976) with forest elements dominating and the presence of *Macaca* as an indicator of a mild climate. The German localities Shernfeld and Deinsdorf 1 (CARLS & RABEDER 1988, 1989) contain mammals characteristic of the temperate forest. In Poland, Kielniki 3B yielded a fauna with mainly open country elements (NADACHOWSKI 1990). Only Sidestrand in England (HARRISON et al. 1989) points to a cold climate, with tundra-forest vegetation. The Villanyian localities of *Lemmus* may represent a considerable time span, but the differences in ecological characteristics of their faunas may also be due to geographical factors. In general, the first immigration of *Lemmus* into Europe took place at a time of mild climates, favourable for the development of forests.

Lemmus continued to be present in Europe into the Early Biharian. There was no radical change in the accompanying fauna, but the first representatives of the subgenus *Allophaiomys*

mys appeared in fossil assemblages. The lineage *Predicrostonyx* – *Dicrostonyx* had not yet reached Europe. In this period *Lemmus* is present in The Netherlands, in faunas 7-9 of the Zuurland borehole (KOLFSCHOTEN 1988), in Poland in Kadzielnia, Kamyk and Kielniki 3A (NADACHOWSKI 1990), in Germany in Neuleiningen 15 (MALEC & TOBIEN 1976) and Hohen-Sülzen (STORCH et al. 1973), in Hungary in Osztramos 2 and 8 (JÁNOSSY 1986), in The Ukraine in Chertkov (REKOVETS 1985), and in Slovakia in Včelare 3 and Chlum 6 (FEJFAR & HORÁČEK 1983).

The paleoecological characteristics of particular local faunas are dependent on their geographical position. In general, they suggest rather mild climates: in Včelare 3, remains of *Macaca* are present. The proportion of species associated with a forest environment was higher in the localities situated further to the west, whereas in the east open-country animals predominated.

The Late Biharian brought important changes to the composition of the rodent fauna in Europe. The appearance of the *Predicrostonyx* – *Dicrostonyx* lineage points to a colder climate. *Allophaiomys* was accompanied by several other subgenera of *Microtus*. *Mimomys savini* was the sole representative of its genus. In Poland, *Lemmus* is known from this period at Zalesiaki 1 (accompanied by *Predicrostonyx*) and in Kozi Grzbiet (with the more advanced *Dicrostonyx simplicior*). In the Romanian locality Betfia 7, *Lemmus* was accompanied by an open country rodent fauna. This is the sole occurrence of lemmings in Romania (TERZEA 1972). In southern Hungary, the locality Somssich Hill 2 (JÁNOSSY 1986) had *Lemmus* in the company of a fauna indicating a mild climate (*Macaca* is present) and an open environment. In Valerots in France, a fauna of similar age included *Dicrostonyx simplicior* but no *Lemmus*. On the other hand, only *Lemmus* was present in West Runton in England (GIBBARD et al., 1991). Grâce à Montières in France yielded both lemmings (BOURDIER et al. 1976) and may belong to the same period. The uppermost part of the Biharian may be represented in the locality Koneprusy C 718 in Bohemia, with both lineages of lemmings present.

The Late Biharian encompasses several climatic cycles well expressed in the vegetational changes registered during the Cromerian. Reconstruction of the changes in the rodent fauna of Europe during particular climatic oscillations is as yet impossible, especially when we keep in mind the important geographical differences in environmental conditions. The precise geological age of many localities from this time remains to be determined.

Younger European rodent localities are characterised by the presence of *Arvicola cantiana* and I shall list all the localities of this period where *Lemmus* is present in the company of that species. Several English localities of this age represent alluvial deposits and do not have a complete representation of the rodent fauna. Nevertheless, they suggest a temperate climate and meadow environment. Remains of *Lemmus* have been found in several of them (Benson, Boxgrove, Hoxne, Swanscombe) (STUART 1982). In France, many micromammalian localities of this period do not contain lemmings. The unique exception is Vergranne, where remains identified as *Myopus schisticolor* have been found (CHALINE et al. 1989). In my opinion the identification of this species cannot be accepted as definitive. Belle Roche in Belgium, a fauna probably originating from the initial phase

of the Holsteinian, contained both lineages of lemmings (CORDY et al. 1990). In Germany there exist numerous fossil localities from this time with remains of *Lemmus* (Karlich Ga, b, H, Erpfingen 1 and 3, Miesenheim I, Mosbach, Petersbuch), while others of similar age lack evidence of this genus (KOENIGSWALD & TOBIEN 1990). *Dicrostonyx* was absent from all these faunal assemblages. The accompanying fauna was a temperate one, not much different in its ecological characteristics from that of the Recent. In Hungary only Tarkö, with a fauna indicating a slightly warmer environment than today, contained both genera of lemmings (JÁNOSSY 1986).

The Saalian glaciation brought with it an important deterioration of the climate of Europe and an immigration of elements characteristic of a cold and arid environment. *Lemmus* was present in many localities in the northern part of the continent. It was found on the Russian Plain, in Poland at Nietoperzowa Cave (layers 15-16), in Germany at Oppurg (layer 9; HEINRICH 1990), Ariendorf (KOLFSCHOTEN 1990) and Hunas (HELLER 1983). In the Netherlands the only locality is Maastricht-Belvedere (KOLFSCHOTEN 1990). *Lemmus* was also found in Britain, in Pontnewydd Cave and Tornewton Cave (Glutton and Bear strata; SUTCLIFFE & KOWALSKI 1976). In France, only two of numerous rodent localities from this time have yielded lemmings: Fage à Noailles and Vaufrey. In most of these localities *Dicrostonyx* was also present, and the accompanying fauna generally had a steppic character, with *Lagurus lagurus* present.

As far as we know, lemmings were not present in Europe during the Eemian interglacial. They appeared once more in the last (Vistulian) glaciation. *Lemmus* is known from numerous localities of this time, reaching from the eastern limits of the European continent to the Atlantic. It is known from Norway (LARSEN et al. 1987) and Denmark, from Poland, Germany, France, Belgium and the Netherlands (KOLFSCHOTEN & JONG 1991), as well as from Britain and Ireland. It did not reach far south in eastern Europe, being unknown from this time in Hungary and Romania. It was usually associated with *Dicrostonyx* and other arctic and steppic elements. It disappeared at the very end of the last glaciation, in eastern Europe usually slightly before the disappearance of *Dicrostonyx*.

Today, *Lemmus* populates the Arctic tundra (and in Scandinavia also montane regions), where it prefers humid environments. Some of its representatives, especially *L. (Myopus) schisticolor*, live in boreal forests (taiga). Its distribution encompasses northern Europe, northern Asia and arctic parts of North America.

III. DICROSTONYCHINAE

The collared lemmings (Dicrostonychinae) represent an evolutionary lineage in which the molars undergo rapid evolution towards a more complicated structure of the grinding surface. Some species in the recent fauna represent a slightly different level of molar evolution. Geologically younger populations have a greater share of more complicated morphotypes. Recent and fossil local populations include different proportions of the various molar morphotypes. The numerous nominal taxa of collared lemmings established for fossil populations are rather misleading. Some were created on the basis of unique specimens (e. g., *Dicrostonyx andaluciensis*) and in such a case nothing can be said about

the evolutionary level of the population they represent. In other cases, species or subspecies are based on the proportion of morphotypes (e.g. *D. intermedius*, *D. gulielmi rotundus*). In this case identification of the taxon is possible only when we have to do with numerous samples of specimens (AGADJANIAN & KOENIGSWALD 1977).

The oldest collared lemmings have been described under the generic name *Predicrostonyx*. They are known from the Cape Deceit locality in Alaska (GUTHRIE & MATTHEWS 1971; *P. deceitensis*) and from localities of the Olyor suite in northernmost Asia (SHER 1992; *P. compitalis*). Both these Beringian forms have been discovered in the company of a fauna indicative of a cold environment and containing primitive representatives of the genus *Microtus*.

In Europe Dicrostonychinae appeared much later than Lemminae, in the Middle Biharian. *Predicrostonyx* is so far known from Zalesiaki 1A in Poland (NADACHOWSKI 1992), Valerots in France (CHALINE et al. 1985), and perhaps also from Včelare 4 in Bohemia (FEJFAR & HORÁČEK 1983). The accompanying fauna suggests that these localities are similar in age, with two species of *Mimomys* and the subgenus *Allophaiomys* present. Their paleoecological characteristics differ slightly, due to their different geographical circumstances: in Zalesiaki open country rodents prevailed, with only a few elements of the boreal forest: *Clethrionomys*, *Apodemus* and, probably, flying squirrels were present. In Valerots there were, besides the arctic elements, also species indicating a milder climate, e. g., several glirids. All these localities may represent the Menapian cold stage.

It is still difficult to correlate the localities of the Russian Plain with those in middle and western Europe. According to MARKOVA (1984) the fauna of Bogdanovka is from the time of the Don glacial. It includes both lemmings, accompanied by steppe-tundra elements. Several species of *Microtus* were present, but neither *Mimomys* nor *Allophaiomys* have so far been found.

The genus *Dicrostonyx*, represented by molar morphotypes simpler than in Late Pleistocene populations, was present in East Asia at about the same time as, or only slightly later than, *Predicrostonyx*. In Europe, the second wave of immigration of Dicrostonychinae, this time represented by *D. simplicior*, seems to take place during the cold phases of the Late Biharian. Collared lemmings were present in faunal assemblages with late populations of *Mimomys savini* and with the genus *Microtus* already diversified into several lineages, e. g., in Karlich Unit E in Germany (KOLFSCHOTEN 1990).

D. simplicior was found at Kozi Grzbiet in Poland, in the company of a fauna with temperate elements, pointing to a climate slightly milder than today (KOWALSKI 1977, NADACHOWSKI 1985). The fauna of Koneprusy Loc. C 718 in the Czech Republic (FEJFAR 1966), type locality of *D. simplicior*, may also originate from this period.

At several younger localities, collared lemmings were present in the company of *Arvicola cantiana*. One of them is Westbury-sub-Mendip in Britain (ANDREWS 1990), with a rich, temperate fauna of rodents including both meadow and forest elements. Of the same age is Belle Roche in Belgium (CORDY et al. 1990). In Hungary, a *Dicrostonyx* locality of similar age is Tarkö (JÁNOSSY 1986), with open country and forest faunal elements side by side. Abundant *Celtis* fruits point to a mild climate.

Dicrostonyx is known from the Saalian glaciation in several countries in Europe. It was present in Britain, where it was accompanied in Tornewton Cave by an open country, cold climate fauna (SUTCLIFFE & KOWALSKI 1976). On Jersey, in the cave of Cotte St. Brelade, there were, besides collared lemmings, elements pointing to a dry, periglacial environment (CHALINE & BROCHET 1987).

In France *Dicrostonyx* reached the Pyrenées during the Saalian, and is, e. g., present in Fage à Noailles, Vaufrey, Arago, Aldène and Cagny. It was usually accompanied by steppe elements (*Lagurus*, *Marmota*, *Spermophilus*), but forest elements were also present.

In Germany, *Dicrostonyx* of Saalian age is known from Hunas (*D. intermedius* described by HELLER 1983), Ariendorf, and Plaidter-Hummerich (KOLFSCHOTEN 1990). These are faunal assemblages of arctic character. Of similar character is the fauna of Nietoperzowa Cave (layers 15-16) in Poland.

In eastern Europe, *Dicrostonyx* reached further south than *Lemmus* during the Saalian. It is present in Uppony 1 (layers 1-5) and Sutto (layer 10; JÁNOSSY 1986), from which *Lemmus* is absent. Steppic elements dominate in these two faunal assemblages.

For obvious reasons the distribution of *Dicrostonyx* is best known in Europe during the last glaciation (Vistulian). It was present, usually in the company of *Lemmus*, on the Russian Plain, in Poland, Germany, Denmark, Belgium, Luxembourg and the Netherlands. It populated Britain, being known as far north as Scotland and it reached Ireland. In France it reached the Pyrenées and the borders of the Mediterranean zone. It is unknown from the Iberian Peninsula with exception of the cave of Cariguela near Granada, from which a single tooth described by RUIZ BUSTOS & GARCIA SANCHEZ (1977) as representing a new species, *D. andalucensis*, is known. According to the published illustration it does not differ morphologically from the teeth of *D. torquatus*, but its presence so far from the known range of this species is enigmatic. No other arctic elements have been found in this locality.

Further to the east the distribution of *Dicrostonyx* during the Vistulian encompassed Switzerland, Austria, the Czech Republic, Slovakia and Hungary. There is a single find from Slovenia, where a tooth of this species was recognized among the material from Babja Jama (RAKOVEC 1975), with an accompanying fauna including steppic and alpine elements (*Marmota*, *Chionomys*).

Both lemmings survived in Europe until the end of the last glaciation. *Dicrostonyx* generally disappeared later than *Lemmus*. In the Recent fauna *Dicrostonyx* is an inhabitant of the arctic tundra. It prefers dry environments, with a substrate of sand or gravel. Its distribution covers the arctic parts of Europe east of the White Sea, Asia and North America including Greenland.

IV. GENERAL REMARKS

This review of the distribution of the two subfamilies of lemmings permits some general remarks. They have nearly identical distributions in the arctic zone of today,

though they populate different microenvironments. This was not the case in the Pleistocene. Lemminae appeared earlier, and the earliest localities in Europe with the genus *Lemmus* contained a fauna indicative of a mild temperate climate. The genus survived in middle latitudes through all colder and warmer phases of the Early and Middle Pleistocene. During this time it was never numerous, evidently populating habitats of limited extension. It is only since the Saalian that it has become numerous and associated with cold environment biotas. The Eemian was the first period of the Quaternary during which *Lemmus* is missing from temperate regions of Europe.

The *Dicrostonyx* lineage appeared later and has from its appearance in Europe been associated with cold climates. It expanded several times to the south-west in Europe, but was always accompanied by animals indicative of a cold and dry environment. As in the case of *Lemmus* its dependence on arctic conditions became much stronger in later phases of the Pleistocene.

The two lineages also differ in their response to humidity. *Lemmus* reached its southernmost distribution in earlier phases of the Quaternary, accompanied by a fauna indicating a mesic environment. *Dicrostonyx* expanded further to the south than *Lemmus* in the latest periods of the Pleistocene, particularly during the last glaciation, and was accompanied by steppe elements.

Homoiothermic vertebrates are in general not good indicators of the abiotic parameters of their environment and this is also the case with rodents. Invertebrates and heterothermic vertebrates are in many cases directly dependent on such factors as the number of days without frost necessary for completing the full cycle of breeding, or minimal winter temperatures. On the other hand, rodents may tolerate a wide range of temperatures. House mice (*Mus musculus*) may, e. g., survive and breed in cold storage plants once they find abundant food and enough material for the construction of nests.

Rodents can also tolerate different humidities. Their small size makes it possible for them to select microhabitats with conditions very different from those of the macroclimate of particular regions.

In cold climates many rodents survive the winter under the snow cover, in this way avoiding very low temperatures. In deserts they may hide in burrows, where the air is much more humid than outside. Rodents may also select what periods they are active during the circadian cycle; so, e. g., in desert conditions they are strictly nocturnal, in mountain and arctic environments partly diurnal. Other adaptations, e. g., hibernation, are connected with the annual cycle. The dependence of rodents on their environment is therefore determined not only by their morphological characteristics, but also by physiological and behavioural adaptations.

Rodents are climatic indicators only in so far as they are connected with particular types of vegetation. These vegetation types are themselves dependent on the climate. In the cold and temperate parts of the Holarctic this is mainly expressed in the existence of successive vegetation belts: tundra, taiga and, further south, deciduous forests or steppes, depending on the degree of continentality.

The Quaternary was a time of cyclic changes in temperature. We would expect that this resulted in a regular latitudinal shift of vegetation zones and their accompanying fauna.

The succession of different faunal assemblages in successive layers of Quaternary sediments could therefore be interpreted as the result of such a shift. This is only partly correct.

Living conditions for animals on the Recent tundra depend not only on low temperatures and abundance of snow, but also on the fact that this vegetation belt is situated in high latitudes. This means that the short growth season coincides with the polar day. For many animals, among them rodents, activity during daylight hours may be associated with a high risk of predation. During the glaciations the tundra zone was situated in middle latitudes of Eurasia. There was neither polar day nor polar night, and nocturnal animals had a chance of being protected by obscurity during the growth season. This could be one of the reasons for the presence of such rodents as glirids in the company of typical arctic tundra elements in the Pleistocene.

The changes in temperature at the beginning and especially at the end of cold phases of the Quaternary were probably very rapid. A shift in the vegetation zones takes a long time, especially in the case of trees. In the periods of change each species adopts an individualistic response in its distribution according to its requirements and mobility. This was the reason for the existence in many periods of the Quaternary of "mixed" communities composed of elements which today are nowhere sympatric.

The presence of a short period of dominance of steppe elements in Central Europe at the Pleistocene – Holocene transition may be the result of a migration lag of forests from the south after the climatic amelioration. This ephemeral steppe belt was soon replaced by forests.

Another factor influencing the distribution of rodents in the European Quaternary is the cline of aridity from the Atlantic to the border of Asia. Of the two lineages of lemmings, *Dicrostonychinae* are better adapted to dry environments and that is why they reached further south in Europe than *Lemmina* during the later phases of the Pleistocene.

Finally, when reconstructing the paleoenvironment on the basis of fossil rodents we must not forget that they were undergoing rapid evolution during the Quaternary. This evolution can be studied only in the case of morphological (in reality mainly dental) characters. Very little is known about the evolution of physiological and behavioural characters that were probably of importance in determining the ecological niches of particular species. The construction of burrows, composition of food, vulnerability to predation and annual and circadian cycle of activity can undergo evolution, and this can strongly influence the environmental requirements of rodents.

The evolution of each element of the biocoenosis influences the other elements (Red Queen hypothesis). The presence of lemmings (especially from the *Lemmus* lineage) in a broader spectrum of environments in the Early Pleistocene may be the result of the absence of competition from other voles, as lemmings were at that time the only arvicolids with permanently growing molars and therefore able to use green, vegetative parts of plants. In the Late Pleistocene they had numerous competitors in the form of newly developed species of genera *Microtus*, *Arvicol*, *Lagurus* and many others.

Notwithstanding all these reservations, critical study of the Quaternary fauna of rodents is one of our most important tools in the reconstruction of the paleoenvironment.

REFERENCES

- AGADJANIAN A. K., KOENIGSWALD W. v., 1977. Merkmalsverschiebung an der oberen Molaren von *Dicrostonyx* (Rodentia, Mammalia) in Jungquärtar. N. Jb. Geol. Paläont., Abh., **153**(1): 33-49.
- ANDREWS P. 1990. Owls, caves and fossils. Nat. Hist. Mus. publ., London, VIII + 231 pp.
- BOURDIER F., CHALINE J., MUNAULT A. V., PUISSEUR J. J., 1976. La très haute nappe alluviale de la Somme. In: BOURDIER T. (Ed.) – Quaternaire et Paléolithique de la Somme et de la basse Seine. AFEQ, 40-41(3-4): 137-143.
- BURNS J. A. 1980. The brown lemming, *Lemmus sibiricus* (Rodentia, Arvicolidae) in the Late Pleistocene of Alberta and its postglacial dispersal. Canadian J. of Zool., **58**(8): 1507-1511.
- CARLS N., RABEDER G., 1988. Die Arvicoliden (Rodentia, Mammalia) aus dem Ältest-Pleistozän von Schernfeld (Bayern). Beitr. z. Paläont. v. Öster., **14**: 123-237.
- CARLS N., RABEDER G., 1989. Pliozäne und ältestpleistozäne Arvicoliden – Reste (Rodentia, Mammalia) aus Deinsdorf, Fränkische Alb. Beitr. z. Paläont. v. Öster., **15**: 149-158.
- CHALINE J., BROCHET G., 1987. The rodent fauna. In: P. CALLOW, J. M. CORNFOLD (Eds.) – La Cotte de St.-Brelade, 1961-1978. Oecobook, Norwich, pp. 139-143.
- CHALINE J., BRUNET-LECOMTE P., BROCHET G., MARTIN F., 1989. Les lemmings fossiles du genre *Lemmus* (Arvicolidae, Rodentia) dans le Pléistocène de France. Géobios, **22**(5): 613-623.
- CHALINE J., RENAULT-MISKOVSKY J., BROCHET G., CLEMENT-DELS R., JAMMOT D., MAURER-CHAUVERÉ C., BONVALOT J., LANG J., LENEUF N., PASCAL A., 1985. L'aven des Valerots (Nuits - Saint-Georges, Côte d'Or), site de référence du Pléistocène inférieur. Revue de Géol. Dyn. et de Géogr. Phys., **26**(2): 109-118.
- CLOT A., CHALINE J., HEINTZ E., JAMMOT D., MAURER-CHAUVERÉ C., RAGE J.-C., 1976. Montoussé 5 (Hautes Pyrénées), un nouveau remplissage de fissure à faune de vertébrés du Pléistocène inférieur. Géobios, Lyon, **9**(4): 511-514.
- CORDY J.-M., BASTIN B., EK G., GEERAERTS R., OZER A., QUINIF Y., THOREZ J., ULRICH-CLOSSET M., 1990. La Belle-Roche (Sprimont, Belgium): the oldest archaeological site in the Benelux. ERAUL, 1992 (preprint).
- FEJFAR O., 1966. Über zwei neue Säugetiere aus dem Altpleistozän von Böhmen. N. Jb. Geol. Paläont., Mh., **11**: 680-691.
- FEJFAR O., HORÁČEK J., 1983. Zur Entwicklung der Kleinsäugerfaunen im Villanyium und Alt-Biharium auf dem Gebiet der CSSR. Schriftenr. geol. Wiss., Berlin, **19**(20): 111-207.
- GIBBARD P. L., WEST R. G., ZAGWIJN W. H., BALSON P. S., BURGER A. W., FUNNELL B. M., JEFFERY D. H., JONG J. DE, KOLFSCHOTEN T. VAN, LISTER A. M., MEIJER T., NORTON P. E. P., PREECE R. C., ROSE J., STUART A. J., WHITEMAN C. A., ZALASIEWICZ J. A. 1991. Early and Middle Pleistocene correlations in the southern North Sea Basin. Quater. Sc. Rev., **10**: 23-52.
- GUTHRIE R. D., MATTHEWS J. V. Jr. 1971. The Cape Deceit fauna – Early Pleistocene mammalian assemblage from the Alaskan Arctic. Quaternary Res., **1**: 474-510.
- HARRISON D. L., BATES J. J., CLAYDEN J. D. 1989. Occurrence of *Lemmus kowalskii* CARLS and RABEDER, 1988 (Rodentia, Microtinae: *Lemmus*) in the Lower Pleistocene of East Anglia. Acta theriol., **34**(3): 55-65.
- HEINRICH W.-D. 1990. Review of fossil arvicolids (Mammalia, Rodentia) from the Pliocene and Quaternary in the German Democratic Republic. Int. Symp. Evol. Phyl. Biostr. Arvicolids, Praha, pp. 183-200.
- HELLER F. 1983. Die Höhlenruine Hunas bei Hartmannshof (Landkreis Nürnberg Land) – Eine paläontologische und urgeschichtliche Fundstelle aus dem Spät-Riss. Quartär-Bibliothek, Bonn, **4**: 1-407.
- JÁNOSSY D. 1973. The boundary of the Plio-Pleistocene based on the Microvertebrates in North Hungary (Osztramos Locality 7). Vertebr. Hung., **14**: 101-113.
- JÁNOSSY D. 1986. Pleistocene vertebrate faunas of Hungary. Akadém. Kiado, Budapest, 208 pp.
- KOENIGSWALD W. v., MARTIN L. D. 1984. Revision of the fossil and recent Lemminae (Rodentia, Mammalia). Spec. Publ., Carnegie Mus. Natur. Hist., **9**: 122-137.
- KOENIGSWALD W. v., TOBIEN H., 1990. Important arvicolid faunas from the Late Pliocene to Early Holocene in Western Germany. Int. Symp. Evol. Phyl. Biostr. Arvicolids, Praha, pp. 231-254.
- KOLFSCHOTEN T. VAN 1988. The Pleistocene mammalian faunas from the Zuurland boreholes at Brielle, The Netherlands. Meded. Werkg. Tert. Kwart. Geol., **25**(1): 73-86.
- KOLFSCHOTEN T. VAN. 1990. The evolution of the mammal fauna in the Netherlands and the Middle Rhine area (Western Germany), during the Late Middle Pleistocene. Meded. Rijks Geol. Dienst, **43**(3): 1-69.
- KOLFSCHOTEN T. VAN, JONG J. DE. 1991. Lemmingen uit de groeve Rientjes bij Hengelo. Cranium, **8**(1): 35-46.

- KOWALSKI K. 1977. Fossil lemmings (Mammalia, Rodentia) from the Pliocene and Early Pleistocene of Poland. *Acta zool. cracov.*, **22**(7): 297-317.
- LARSEN E., GULLIKSEN S., LAURITSEN S.-E., LIE R., LOVLIE R., MANGERUD J. 1987. Cave stratigraphy in western Norway; multiple Weichselian glaciations and interstadial vertebrate fauna. *Boreas*, **16**: 267-292.
- MALEC F., TOBIEN H. 1976. Die Säugerreste-führenden Spaltenfüllungen des älteren Pleistozäns von Neu-leiningen bei Grünstadt (Pfalz). *Mainzer geowiss. Mitt.*, **5**: 129-134.
- MARKOVA A. K. 1984. Late Pleistocene mammal fauna of the Russian Plain. In: VELICHKO A. A. (Ed.) – Late Quaternary environments of the Soviet Union. Longman, London, pp. 208-218.
- NADACHOWSKI A. 1985. Biharian voles (Arvicolidae, Rodentia, Mammalia) from Kozi Grzbiet (Central Poland). *Acta zool. cracov.*, **29**(2): 13-28.
- NADACHOWSKI A. 1990. Review of fossil Rodentia from Poland (Mammalia). *Senckenbergiana biol.*, **70**(4/6): 229-250.
- NADACHOWSKI A. 1992. Early Pleistocene *Predicrostonyx* (Rodentia, Mammalia) from Poland. *Acta zool. cracov.*, **35**(2): 203-216.
- RAKOVEC J., 1975. [Über Quartäre Säugetierfaunen Sloveniens (NW Jugoslawien)] [Slovenian with German summary]. *Archeoloski Vestnik, Ljubljana*, **24**: 225-270.
- REKOVETS L. J. 1985. [Microtheriofauna of the Desna – Podneprovsk Late Paleolithic] [in Russian]. Kiev, Nauk. Dumka, 166 pp.
- RUIZ BUSTOS A., GARCIA SANCHEZ M. 1977. Las condiciones ecologicas del Musteriense en las Depresiones Granadinas. La fauna de micromamiferos en la cueva de la Cariguela (Piñar, Granada). *Cuadernos Prehist. Granadinos*, **2**: 7-17.
- SHER A. 1992. Beringian fauna and Early Quaternary mammalian dispersal in Eurasia: ecological aspects. *Courier Forsch. – Inst. Senckenberg*, **135**: 125-133.
- STORCH G., FRANZEN J. M., MALEZ F. 1973. Die altpleistozäne Säugerfauna (Mammalia) von Hohensülzen bei Worms. *Senckenberg. Lethaea*, **54**: 311-343.
- STUART A. J. 1982. Pleistocene vertebrates in the British Isles. Longman, London and New York, X + 212 pp.
- SUKHOV V. P. 1976. [Fossil lemmings in the Pleistocene strata of Bashkiria] [In Russian]. In [Rodents, evolution and history of their recent fauna]. *Proc. Zool. Inst. Ac. Sc. USSR*, **66**: 117-121.
- SUTCLIFFE A. J., KOWALSKI K. 1976. Pleistocene rodents of the British Isles. *Bull. Brit. Mus. (N. H.), Geology*, **27**(2): 31-137.
- TERZEA E. 1972. Sur la présence du genre *Lemmus* (Rodentia, Mammalia) dans le Pléistocène de la Roumanie. *Folia quatern.*, **40**: 57-65.